Effects of elevated atmospheric CO_2 on water relations of soya bean

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ABSTRACT

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Soya bean (*Glycine max* (L.) Merr. 'Bragg') plants were grown in large containers in open-top field chambers under five atmospheric CO_2 concentrations (349–946 $\mu l\, l^{-1}$) and two water regimes. Rate of soil water depletion for the high CO_2 treatments started to decrease under well-watered conditions during anthesis and by early pod formation under water-stressed conditions. During reproductive growth, normal and stressed plants at 349 $\mu l\, l^{-1}$ (ambient level) received irrigation water 29 and 12 times, respectively, compared with 21 and 9 times, respectively, at 946 $\mu l\, l^{-1}$ CO_2. At both anthesis and pod fill, plants grown under CO_2 enrichment exhibited greater leaf area. Nevertheless, water use per plant either remained constant (stressed plants at anthesis) or else declined (well-watered plants at anthesis; both moisture levels during pod fill) in response to CO_2 enrichment. At pod fill, leaves of CO_2-enriched plants generally displayed a higher stomatal resistance, except near the end of the sampling period when a sudden increase in resistance was observed under low CO_2 owing to low soil water availability. Midday xylem potential for well-watered plants was greater than values for stressed plants and was unaffected by CO_2 treatment. Under low moisture conditions, elevated CO_2 had no effect on xylem potential at anthesis; however, during pod fill potential increased significantly with increasing CO_2 concentration, as elevated CO_2 decreased water use rates, lowering soil water stress. Alleviation of water stress during critical reproductive phases was strongly suggested.

INTRODUCTION

The concentration of CO_2 in the atmosphere is known to be rising (Keeling et al., 1989), and if the current trend continues, a doubling of the present concentration ($\sim 350 \mu l\, l^{-1}$) may occur during the next century (Gribbin, 1981). Although CO_2 is only a trace gas in the atmosphere, increases in its concentration could significantly affect global agriculture. Carbon dioxide is essential to plant growth as a source of carbon necessary for photosynthesis

and influences stomatal opening, hence affecting water vapor and gas exchanges. For a great many plant species, CO_2 enrichment is known to increase dry matter production and frequently increases net photosynthesis (Rogers et al., 1983a; Sionit et al., 1984; Strain and Cure, 1985; Allen et al., 1987; Warrick, 1988; Allen, 1990). Increased CO_2 levels induce stomatal closure, thereby decreasing transpiration rate which enhances water use efficiency (Carlson and Bazzaz, 1980; Kimball and Idso, 1983; Dahlman et al., 1985). On the other hand, the availability of soil water to crops is considered to be the major limitation to crop production in the U.S. (Boyer, 1982). Generally speaking, plant growth is reduced under soil water deficits owing to decreases in water potential, stomatal aperture, and photosynthesis (Boyer, 1970).

Consequently, research investigations have sought to evaluate the interactions of elevated CO_2 and limited soil water. Growth chamber studies with wheat (*Triticum aestivum* L.) have demonstrated that owing to the influence of CO_2 on water use efficiency (Gifford, 1979) and on water stress adaptation through osmoregulation (Sionit et al., 1981), enhancement of dry matter production under water stress conditions still occurs under CO_2 enrichment. Soya beans grown under CO_2 enrichment and subjected to water stress during early reproductive growth avoided the onset of severe water stress by exhibiting decreased water use (Rogers et al., 1984) and increased water use efficiency (Huber et al., 1984), thus enabling them to maintain higher leaf water potentials compared with those under low CO_2. The results of these studies and the paucity of data on closely monitored long-term field studies on CO_2 and water stress interaction conducted where soil water was restricted throughout the soya bean growth cycle warrants further investigation. The objective of this study was to help fill that knowledge gap.

In the present work, soya bean plants were grown in large containers in open-top field chambers under various CO_2 levels and subjected to repeated drying cycles for the entire growing season. More specifically, the objectives of this investigation were : (a) to study the influence of these treatments on leaf water potential, stomatal resistance, and transpiration; (b) to document the influence of CO_2 concentration on water use of well-watered and water-stressed plants at two periods in reproductive growth; (c) to determine the relationship of leaf area and rate of water use at these same periods.

MATERIALS AND METHODS

Soya bean plants were grown from seeds in containers placed in open-top field chambers (Rogers et al., 1983b) at different atmospheric CO_2 concentrations and in open plots (i.e., no chambers) under ambient atmospheric conditions. Each chamber was constructed of a cylindrical aluminum frame (3 m in diameter by 2.4 m in height) covered with PVC film panels (Roll-A-

Glass*) with a 45° frustum attached at the top; panels were held to the frame in farthingale fashion. Air with a predetermined amount of CO$_2$ was supplied continuously at 0.94 m^3 s^{-1} through the perforated inner wall of the double-walled bottom half of each chamber. There were two replicates of six CO$_2$ treatments. Seasonal daytime CO$_2$ means ± 1 SD were: 348 ± 19 (ambient plots without chambers), 349 ± 19 (ambient chamber), 421 ± 22, 496 ± 24, 645 ± 33, and 946 ± 49 μl l^{-1} (enriched chambers). A microcomputer was used to control the automatic delivery of air samples to a nondispersive infrared CO$_2$ analyzer, to log data, and to assist in regulating the injection of CO$_2$.

Seeds were inoculated with commercial *Rhizobium* and planted on Julian Day 172 in large plastic containers (16.5 l) containing 13 l of a 2:1:1 mixture (by volume) of sandy clay loam soil: sand: *Metro-Mix 220 (W.R. Grace Co.). Each study plot (chamber or open plot) contained 20 plants grown singly in containers which were randomly divided into two groups of 10 and subjected to two watering regimes. Differential water treatments were monitored with tensiometers, and rain was excluded by the erection of a removable transparent plastic covering during periods of rainfall. Containers were placed on racks to ensure proper drainage and exclude any groundwater. Plants were rewatered when tensiometers reached −0.005 to −0.015 MPa and −0.075 to −0.085 MPa for well-watered controls (WW; $N=4$) and water-stressed (WS; $N=6$) plants, respectively. Monitoring of drying cycles started when plants were at the third-node stage (V-3; Fehr and Caviness, 1977). Tensiometer readings (taken three times each day) and intervals between watering were recorded for the entire season. All tensiometers were flushed to eliminate air bubbles and refilled with degassed water each week. One liter of an N-free nutrient solution (Israel, 1981) was added to every container once a week.

The experimental design was a split plot with a randomized complete block arrangement of the main-plot factor (test atmospheres of CO$_2$) for which there were two blocks. The treatments of the second factor (water treatments: WW and WS) were randomly assigned to subplots (containers) within each main plot.

Leaf transpiration, stomatal resistance, xylem pressure potential (Ψ_x) and whole canopy transpiration (water use) measurements were made at two periods in reproductive growth: anthesis (RI) and pod fill (R5). All containers were watered to drip-point and WS plants were then allowed to go through a drying cycle while WW plants received irrigation water as needed. Corresponding drying cycles for RI and R5 occurred 55–61 and 94–102 days after planting (Fig. 1).

Leaf transpiration and stomatal resistance were determined with a LI-COR

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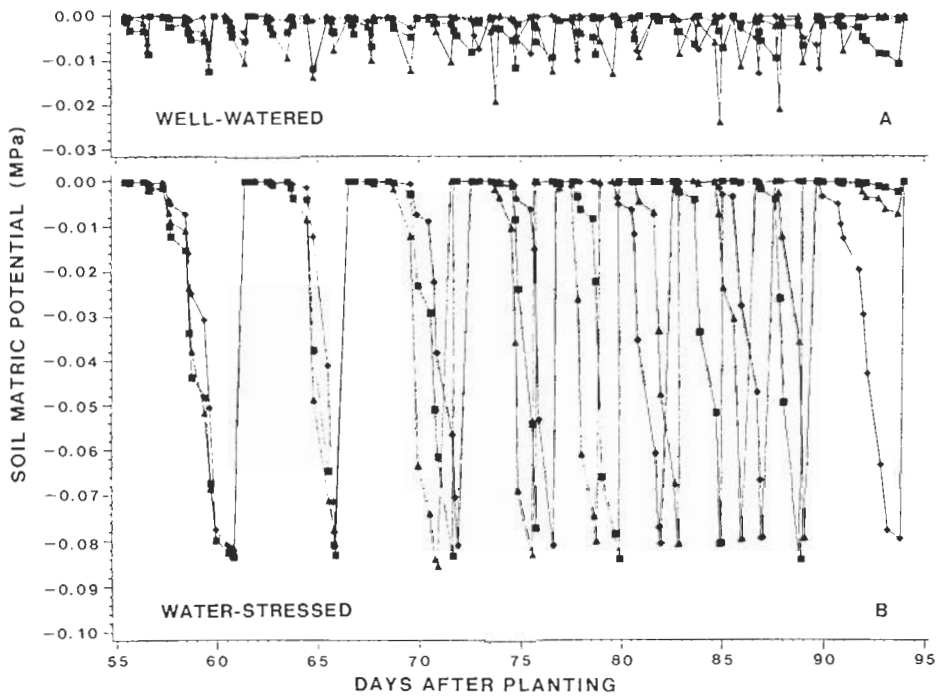
Fig. 1. Changes in soil matric potential (A,B) during reproductive growth (55–94 days after planting) for well-watered and water-stressed soya bean grown at 349 ($\blacktriangle$), 645 ($\blacksquare$) and 946 ($\blacklozenge$) $\mu l \, l^{-1}$. For WW, $N=4$; for WS, $N=6$.

1600 Steady State Diffusive Resistance Porometer. At R5, daily measures were made on eight plants (four WW and four WS) per plot for both blocks. All measurements were obtained from the abaxial surface of fully expanded, sun-exposed trifoliates at the canopy top between 13:00 and 14:00 h.

A pressure chamber apparatus (PMS Instrument Co.) was used to measure xylem potential (Ψ_x). At R1, readings were made at the end of the drying cycle. However, by R5, WS plants at the lower CO_2 levels (348–496 $\mu l \, l^{-1}$) were depleting soil water faster than the high CO_2 level plants; therefore, in order to make direct comparisons of plant water status at the various CO_2 values, measurements of Ψ_x were made for all treatments prior to rewatering those with lower CO_2. Values of Ψ_x were taken from six plants (three WW and three WS) in each plot.

Water use was determined gravimetrically during the two sampling periods with a digital weighing scale. A total of six containers (three WW and three WS) from each plot were weighed every 24 h during the sampling periods. Leaf areas were obtained photometrically on these same plants. Thus, water use could then be expressed on both a per plant and a per unit leaf area basis.

Statistical analyses of data were performed according to standard analysis

of variance (ANOVA) and regression techniques using Statistical Analysis Systems (1985). All tests of statistical significance were conducted at $P < 0.05$.

RESULTS AND DISCUSSION

Observations from three drying cycles during vegetative growth (data not shown) and the first two drying cycles in early reproductive phase (Fig. 1b) indicated that WS soya beans grown under the various CO$_2$ levels extracted soil water at similar rates. In addition, it was observed that vegetative drying cycles (data not shown) were approximately twice as long as those occurring in the early part of the reproductive period (Fig. 1b). Thus, there was a clear indication that soil water depletion had accelerated at the onset of reproduction. Similar observations have been made by other researchers studying soya bean under ambient levels of CO$_2$ (Teare et al., 1973; Kanemasu et al., 1976).

During reproductive growth, the positive effects of CO$_2$ enrichment on soil water conservations were observed earlier under the WW regimes than under the WS condition (Fig. 1a,b; see also Fig. 3a). Although high-CO$_2$ grown plants were larger, water extraction from the soil proceeded at a much lower rate. For example, under WS conditions on Day 70, the 349 μl l^{-1} treatment reached the end of a drying cycle before the 645 or the 946 μl l^{-1} treatment. High CO$_2$ plants encountered the same low water a few days later, but as the watering cycle was longer, these plants experienced fewer stressful days than low CO$_2$ plants over the season. Subsequent drying cycles were out of phase until rewatering on Day 94 (Fig. 2). Within this period, all plants were at the R5 stage. The initial drying cycle for both water treatments shown in Fig. 2b clearly demonstrates that plants grown under 645 and 946 μl l^{-1} CO$_2$ had lower rates of soil water depletion than plants grown at 349 μl l^{-1} CO$_2$.

Overall, during reproductive growth, WS plants at 349 μl l^{-1} CO$_2$ went through 12 drying cycles compared with 10 and 9 at 645 and 946 μl l^{-1} CO$_2$, respectively. Under WW conditions, plants grown at 349 μl l^{-1} CO$_2$ received irrigation water 29 times compared with 24 and 21 times at 645 and 946 μl l^{-1} CO$_2$, respectively. Based on these observed values, we can infer that CO$_2$ enrichment has a strong tendency to alleviate plant water stress when critical periods of water demand occur during reproduction. Previous work has demonstrated that soya bean is more sensitive to water stress during pod and seed development than during vegetative growth (Sionit and Kramer, 1977; Korte et al., 1983). In order to examine this phenomenon at different levels of CO$_2$, we examined in detail two periods during reproductive growth (R1 and R5).

Total leaf area and rates of water use per plant and per unit leaf area as affected by water regime and CO$_2$ concentration during two periods within the reproductive phase are shown in Figs. 3 and 4. At R1, water use per plant declined linearly with increasing CO$_2$ under WW conditions (Fig. 3a). Based on regression values from the 349 and 946 μl l^{-1} treatments, we observed an
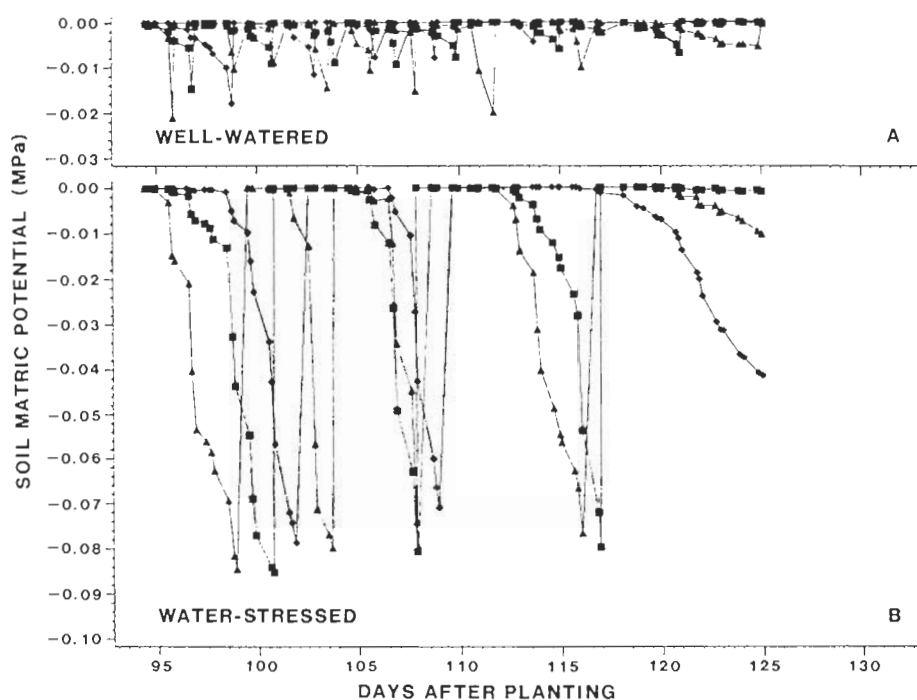
Fig. 2. Changes in soil matric potential (A,B) during reproductive growth (>94 days after planting) for well-watered and water-stressed soya bean grown at 349 (▲), 645 (■) and 946 (♦) $\mu l \, l^{-1}$. For WW, $N=4$; for WS, $N=6$.

approximate 15% reduction in plant water use. Decreases in water use per plant were documented even though plants grown under CO_2 enrichment exhibited significant increases in leaf area (Fig. 3c). Leaf area was 27% greater at 946 than at 349 $\mu l \, l^{-1}$. Thus, a more striking decrease in canopy transpiration was observed when water use was expressed on a unit leaf area basis (Fig. 3b). Rate of water use per unit leaf area was reduced by 47% at the 946 $\mu l \, l^{-1}$ treatment level compared with the 349 $\mu l \, l^{-1}$ control.

As expected, water stress significantly reduced rates of water use and leaf area at all levels of CO_2, relative to WW controls. More importantly, the rate of water use per plant was unaffected by CO_2 treatment (Fig. 3a). In fact, plant water use remained relatively constant across the various CO_2 treatment levels. These data verified observations from corresponding WS drying cycles which demonstrated that additional CO_2 had no effect on reducing rates of soil water depletion (Days 55–61; Fig. 1b). On the other hand, leaf area increased linearly in response to elevated CO_2 (Fig. 3c). Therefore, water use expressed on a unit leaf area basis exhibited a significant decrease (Fig. 3b). Water use per unit leaf area in plants at 946 $\mu l \, l^{-1}$ CO_2 was 27% less than in those of the 349 $\mu l \, l^{-1}$ control.

At R5, water use per plant decreased linearly for both water regimes in re-
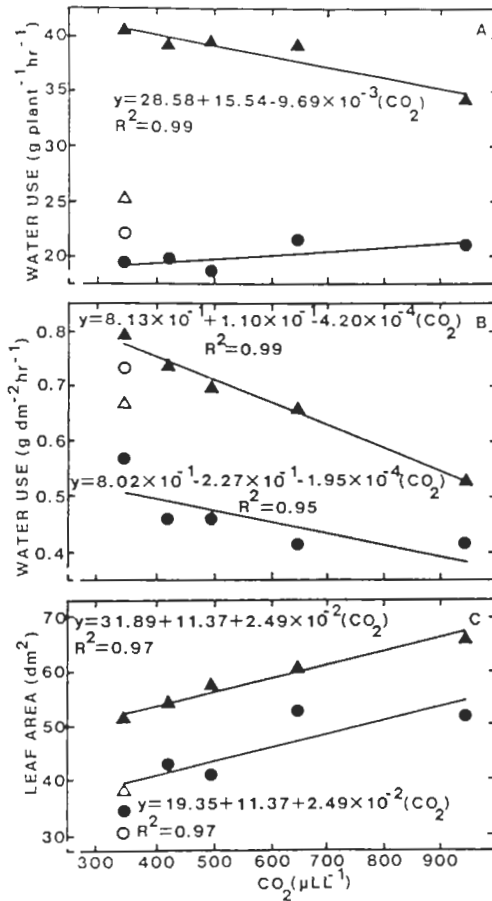
Fig. 3. Water use per plant (A) and per unit leaf area (B) and leaf area per plant (C) for well-watered ($\triangle$, $\blacktriangle$) and water-stressed ($\bigcirc$, $\bullet$) soya bean grown in open plots (open symbols) and five CO$_2$ treatments within chambers (closed symbols) at anthesis. Second term in the best fit linear regression equation represents significant chamber effect. Response to CO$_2$ was non-significant for WS in A. $N=6$.

sponse to increased CO$_2$ (Fig. 4a). These data reinforced findings from corresponding drying cycles which indicated that soil water extraction proceeded at a much lower rate under CO$_2$ enrichment (Days 94–102; Fig. 2b). We found no significant stress by CO$_2$ interaction, suggesting that plants in both water treatments had similar responses to additional CO$_2$. Each water stress treatment reduced water use per plant by approximately the same proportion at each CO$_2$ level. Based on regression values from the 349 and 946 $\mu l\ l^{-1}$ treatment levels, water use per plant was reduced by about 32% at the high CO$_2$ level in both water treatments.

In terms of leaf area, we observed a highly significant stress by CO$_2$ interaction (Fig. 4c). Chronic water stress reduced leaf area. However, the adverse effects were most noticeable at the lower two treatment levels (349 and
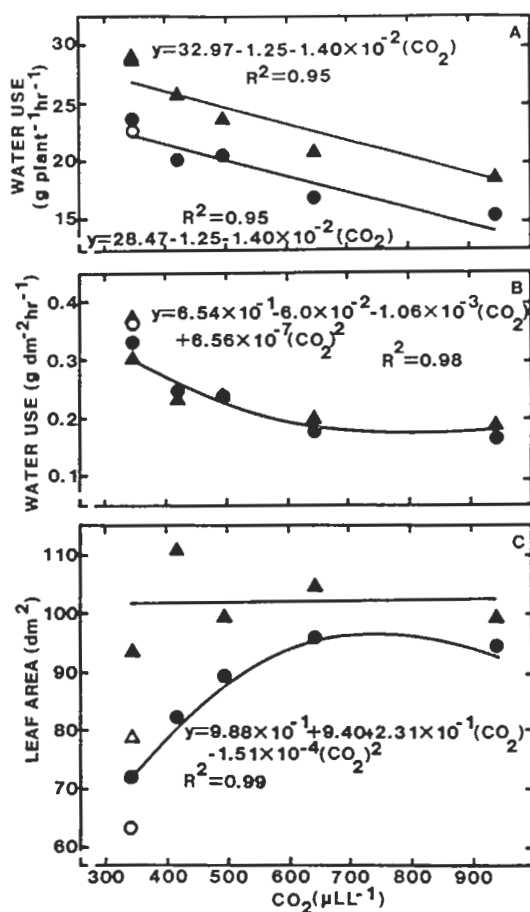
Fig. 4. Water use per plant (A) and per unit leaf area (B) and leaf area per plant (C) for well-watered ($\triangle$, $\blacktriangle$) and water-stressed ($\bigcirc$, $\bullet$) soya bean grown in open plots (open symbols) and five CO_2 treatments within chambers (closed symbols) at pod fill. Best fit linear and quadratic regression lines are shown. Chamber effect (second equation term) was significant in B and C. Response to CO_2 model was non-significant for WW in C. $N=6$.

421 $\mu l\ l^{-1}$). WW plants showed a slight but not statistically significant increase in leaf area as CO_2 was increased. In contrast, the leaf area of WS plants increased progressively with increasing CO_2 up to 645 $\mu l\ l^{-1}$. Values of leaf area at both the 645 and 946 $\mu l\ l^{-1}$ steps were essentially the same. Leaf area was 32% higher in soya bean plants grown at 645 $\mu l\ l^{-1}$ CO_2 than in those grown at 349 $\mu l\ l^{-1}$. However, when water use was expressed on a unit leaf area basis, CO_2 was the only significant source of variation (Fig. 4b). Rates of water use per unit leaf area declined in a nonlinear fashion with increasing CO_2. Values at 645 and 946 $\mu l\ l^{-1}$ CO_2 were approximately 40% lower than at the 349 $\mu l\ l^{-1}$ control.

It is important to note that increased leaf area due to CO_2 under WS conditions (Fig. 3c) may have counteracted high stomatal resistance per unit leaf

area (data not shown). Nevertheless, whole canopy rate of water use (Fig. 3a) remained relatively unchanged with rising CO_2. Similar results were obtained by Jones et al. (1984) working with soya bean at similar ages grown under optimal soil water conditions. These investigators found that diurnal bulk canopy resistance (stomatal plus boundary layer) was greater for high CO_2 soya bean canopies, but that this was offset by a larger transpiring leaf area and higher vapor pressure deficits. They further observed that absolute water use was approximately the same across various CO_2 concentrations. Likewise, in a growth chamber study, Gifford (1979) reported little change in the actual amount of water used by wheat grown under CO_2 enrichment and different water regimes. Conversely, in agreement with observations reported by Rogers et al. (1984), the increase in leaf area (Fig. 3c) under WW conditions was apparently not sufficient to offset the high stomatal resistance per unit area (data not shown), thus total canopy water use rate decreased (Fig. 3a) with increasing CO_2 concentration.

Figure 5 illustrates the effects of CO_2, and water treatment on leaf stomatal resistance and transpiration over several days at R5. As reported elsewhere for other species (Carlson and Bazzaz, 1980; Patterson and Flint, 1982), throughout the sampling period, leaves of CO_2 enriched plants grown under WW conditions had higher stomatal resistance (Fig. 5a) and lower transpir-
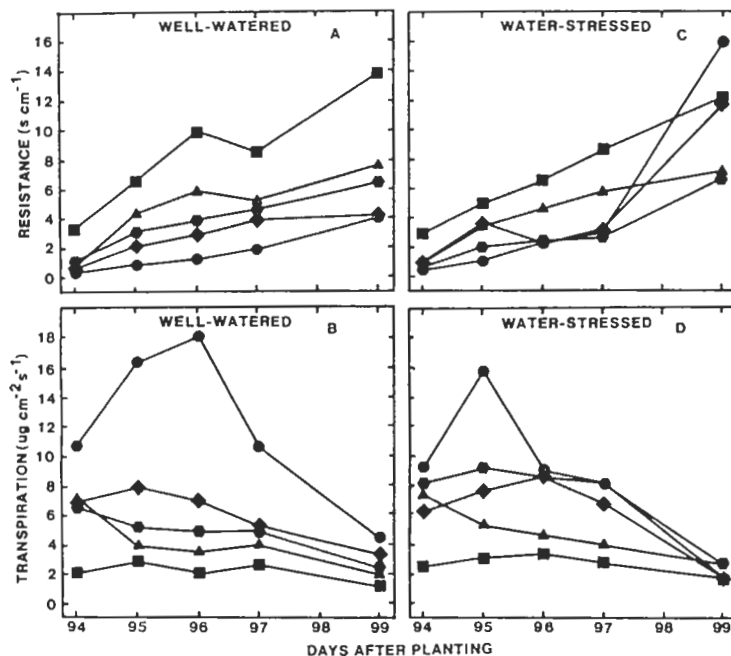

Fig. 5. Leaf stomatal resistance (A,C) and transpiration (B,D) for well-watered (A,B) and water-stressed (C,D) soya bean grown in five CO_2 treatments within chambers (●, 349; ◆, 421; ●, 496; ▲, 645; ■, 946 μl l^{-1}) at pod fill. Measurements were taken for 6 days during a drying cycle (Days 94–102). $N=8$.

ation rates (Fig. 5b) relative to those WW plants in ambient CO_2. Under WS conditions, the stomatal response at 645 and 946 μl l^{-1} CO_2 (Fig. 5c) resulted in transpiration rates (Fig. 5d) which were similar to those observed under WW conditions (Fig. 5b). Even during early portions of stress periods, lower levels of elevated CO_2 (421 and 496 μl l^{-1}) induced partial stomatal closure which caused lower transpiration rates relative to the 349 μl l^{-1} control. However, from Day 3 onward, soya beans grown at 349–496 μl l^{-1} CO_2, exhibited similar decreases in transpiration rate in response to decreasing water availability. Likewise, the sudden rise in stomatal resistance observed at 349–496 μl l^{-1} CO_2 on Day 6 (Fig. 5d) reflects plant response (i.e., stomatal closure) to low soil water availability. Similar to observations reported by Rogers et al. (1984), transpiration at all CO_2 levels fell to nearly the same low rate on this day despite the large differences in resistance.

Midday Ψ_x data from both reproductive periods are shown in Fig. 6. At R1, CO_2 enrichment had little effect on reducing Ψ_x under water stress (Fig. 6a). The fact that similar midday stresses were seen was not surprising since plants at the various CO_2 concentrations had extracted soil water at equivalent rates (Fig. 3a) and therefore reached approximately the same soil moisture level by the time of measurement (Day 60; Fig. 1b). For WW plants, there were no significant differences in Ψ_x due to CO_2. Comparable results have been reported for soya bean, sicklepod (*Cassia obtusifolia* L.), and showy crota-
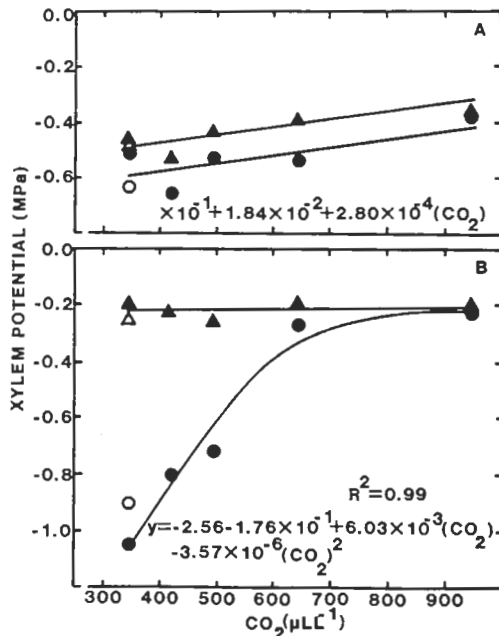

Fig. 6. Leaf xylem potential for well-watered ($\triangle$, $\blacktriangle$) and water-stressed ($\bigcirc$, $\bullet$) soya bean grown in open plots (open symbols) and five CO_2 treatments within chambers (closed symbols at anthesis (A: Day 60) and pod fill (B: Day 94). Best fit lines are shown. Chamber effect was not significant. Response to CO_2 was non-significant in A and for WW in B. $N=6$.

laria (*Crotalaria spectabilis* Roth) measured 35 days after planting (Patterson and Flint, 1982). A significant stress effect was detected; however, the actual magnitudes of Ψ_x for WS plants were not much lower than WW plants, the differences in soil water notwithstanding. Evaporative demands at this sampling period were such that any difference in Ψ_x due to soil water or CO$_2$ level should have been detected. Therefore, the small observed differences in Ψ_x were probably due to plant size and soil water deficits being too low to cause a substantial difference in plant water deficit at this growth stage (Sionit and Kramer, 1976).

At R5 we observed a well-defined water stress by CO$_2$ interaction (Fig. 6b). There was little difference in Ψ_x due to CO$_2$ under WW conditions. In contrast, under WS conditions, Ψ_x increased significantly with rises in CO$_2$. This response is confirmed when one recalls that WS plants grown under elevated CO$_2$ had lower rates of water use (Fig. 4a) and thus were under a lower level of stress (Fig. 2b). Plants grown at 349, 421 and 496 μl l^{-1} CO$_2$ had Ψ_x values of -1.08, -0.83, and -0.72 MPa, respectively. Although Boyer (1970) and Ghorashy et al. (1971) reported that leaf water potentials below -1.1 MPa were necessary to inhibit photosynthesis of young soya bean leaves, the values of Ψ_x attained by WS plants grown at these CO$_2$ levels were probably low enough to inhibit afternoon photosynthesis as wilting (as evidenced by severe flagging of leaves) was observed at these treatment levels. Wilted leaves recovered completely after rewatering. On the other hand, as the soil water levels were still relatively high (Fig. 2b) under WS conditions at the 645 and 946 μl l^{-1} levels, their respective Ψ_x values were similar to their WW control values (Fig. 6b). Likewise, others have reported that the water potential of soya bean (Rogers et al., 1984) and wheat (Sionit et al., 1981) growing under low CO$_2$ concentrations declined more rapidly and reached a lower value at the end of the stress period relative to those grown under high CO$_2$. In the present study, high CO$_2$ plants showed no signs of wilting at this time or when the plants reached a similar low soil water level a few days later (data not shown). Ambient grown plants showed extensive wilting at a time when other environmental factors are most conducive to rapid carbon fixation; thus, plants grown at high CO$_2$ presumably have an advantage over plants grown at a lower CO$_2$ level.

The results from this field experiment (conducted with soya bean plants grown in large containers) strongly indicates that the benefit of additional CO$_2$ on reducing the rate of water consumption occurs primarily at the beginning of reproductive growth (R1–R2) under WW conditions, but is delayed until the R3 stage under WS conditions. Detailed measurements from two stages in reproductive growth (R1 and R5) clearly showed that larger plants produced as a result of CO$_2$ enrichment generally had more leaf surface area. However, this was not sufficient to counteract the lower rate of transpiration per unit leaf area. Water use per plant either remained constant (WS plants

at R1) or declined (WW plants at R1; WW and WS plants at R5) in response to CO_2 enrichment. Our results suggest that a decreased rate of water use could, in itself, alleviate water deficit in soya bean at critical periods of water demand during reproductive growth. Reduced water use coupled with increases in dry matter production as also reported elsewhere for soya bean (Rogers et al., 1986) and other plants (Kimball, 1983) could lead to increases in water use efficiency which would have a substantial impact on agricultural productivity. However, further research with various economically important species grown in conventional row systems and under higher levels of soil water stress will be required in order to make accurate predictions concerning the potential effects of elevated atmospheric CO_2 on crop water use.

ACKNOWLEDGMENTS

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